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A CONTRIBUTION TO KNOWLEDGE OF PHRAGMITES (GRAMINEAE) IN SOUTH AFRICA, WITH PARTICULAR REFERENCE TO NATAL POPULATIONS

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ABSTRACT

A study of populations of *Phragmites*, in Natal, revealed differences in vegetative structure, epidermal features, chromosome numbers, habitat preferences and distributional patterns, between *P. mauritianus* Kunth and *P. australis* (Cav.) Trin. ex Steud.

Some of these differences facilitate identification of the two species, especially in the field. The habitat preferences are significant in relation to ecological changes, particularly siltation, in swamps and estuaries.

UITTREKSEL

'n BYDRAE TOT DIE KENNIS VAN *PHRAGMITES* (GRAMINEAE) IN SUID-AFRIKA, MET SPESIALE VERWYSING NA DIE NATAL POPULASIES.

'n Studie van Natalse *Phragmites* populasies het die volgende feite aan die lig gebring: naamlik, dat *P. mauritianus* Kunth en *P. australis* (Cav.) Trin. ex Steud. van mekaar verskil ten opsigte van vegetatiewe-samestelling, epidermale-kenmerke, chromosoomgetal, habitatsvoorkeur en verspreidingspatroon.

Sommige van hierdie verskille vergemaklik identifikasie van die twee soorte in die veld. Hulle habitatsvoorkeur is betekenisvol ten opsigte van ekologiese veranderinge, in besonder ten opsigte van toeslikking in moerasse en riviermonde.

The reed, *Phragmites* Adan. (Gramineae, Arundineae) is common along river and stream banks in South Africa. Chippindall (1955) recorded *P. communis* Trin. and *P. mauritianus* Kunth for the Republic and stated that the former was widespread, the latter, without record from the Cape Province, was more tropical. The relative length and width of the glumes was considered the most reliable means of distinguishing between these species.

Clayton (1967), in considering the genus on a world basis, concluded that from among the "... very large number of species and infra-specific taxa ... described ...", three allopatric species should be recognized. All three, according to this author, are represented on the African continent. *P. karka* (Retz.) Trin. ex Steud. in Ethiopia, the Sudan and West Africa, with rare specimens in Kenya and Uganda. *P. mauritianus* Kunth in Tropical Africa, the northern limit passing through Ethiopia, the Sudan and the Congo; no southern limit being stipulated. *P. australis* (Cav.) Trin. ex Steud. = [*P. communis* Trin.] (Clayton, 1968), with subspecies *altissimus* (Benth.) Clayton limited to the Medi-

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terranean shores, the southern edge of the Sahara, Ethiopia and Kenya, and subspecies *australis* in temperate regions of both hemispheres (which would include South Africa). Clayton stressed that the three species ". . . cannot be readily separated by any single character," so that it is essential to assess the distinguishing features as a whole.

Undoubtedly both *P. mauritianus* and *P. australis* subspecies *australis* grow in Natal, but neither the glume parameters recommended by Chippindall, nor the broader plexus of distinguishing characters advocated by Clayton, nor other available keys such as that of Sturgeon (1954) relating to Rhodesian grasses, engendered full confidence in attempting to identify flowering herbarium specimens. Sterile material was even more uncertain.

As populations were readily available for study, a field and laboratory investigation was undertaken to determine whether living plants could be identified more easily than dried material, and whether additional criteria might be detected that would make distinctions between established taxa more conclusive. At the same time, attention was paid to variation within and between populations, and to the general ecological conditions under which plants grew, as far as these could be simply assessed. Lastly the distributional range, particularly in Natal, was recorded.

STUDY OF POPULATIONS

A: *In the Field*

1. *Sampling. Phragmites*, in South Africa, flowers in late summer and autumn. During these seasons, populations were located, studied and sampled. The populations considered in detail were mostly in Natal, from the coast and midlands. Up to twenty stems (approximately three quarters in flower, one quarter sterile) from each population were dug out or cut close to ground level, then folded into presses to serve as reference samples for subsequent laboratory study. As far as possible, the stems taken represented specimens grading from the fringe to more deeply into a population, so as to cover a representative range of habitat conditions, but it was sometimes difficult to penetrate far where plants grew in water. Representative material (mature leaves borne at half to two-thirds the height of the flowering stem, well developed inflorescences, young axillary buds and roots) were fixed in recommended fixatives for subsequent floral, anatomical and cytological study.

In addition to initial location and study, many of the populations were re-visited at other seasons, so that observations could be made at different stages in the life-cycle. Also new populations from the Transvaal to the Cape were located from time to time and observations made. Herbarium specimens from widely differing localities were also examined for purposes of comparison with living plants and to supplement distributional records.

2. *Results of Gross Morphological Study.* Field study soon revealed that the species were distinct under natural conditions and could generally be recognized quite readily: especially was this so at the peak of the flowering season when inflorescences were numerous and in good condition.

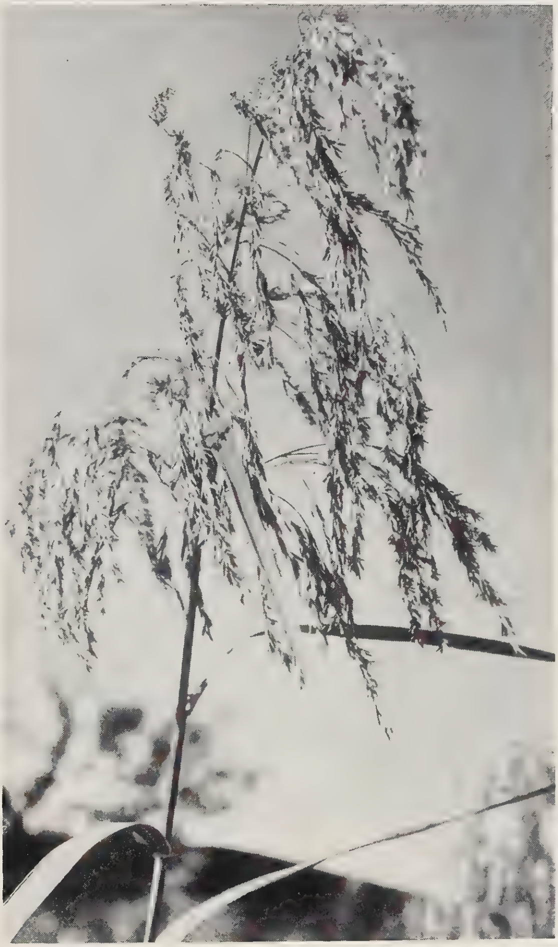

FIG. 1.
Phragmites mauritianus: inflorescence.

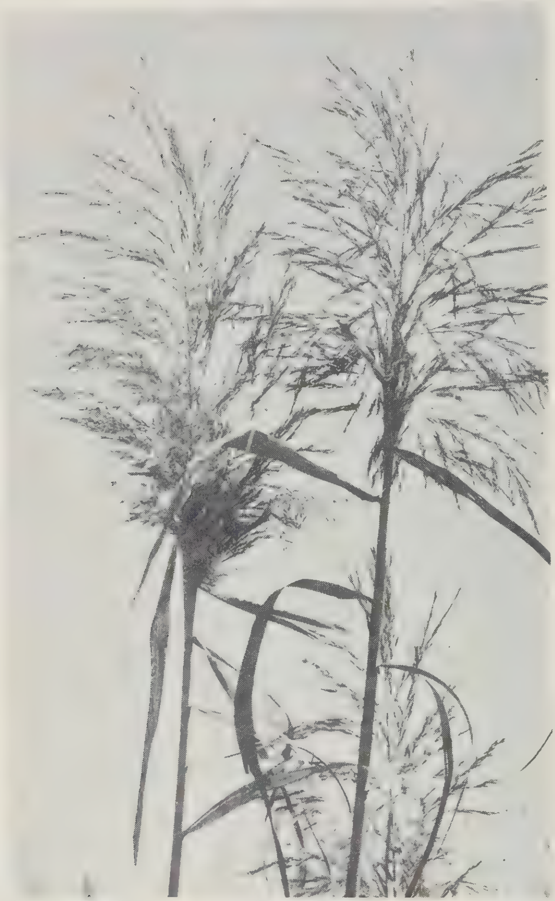

FIG. 2.
Phragmites australis: inflorescences (note stem to the left with leaves, except the uppermost, arranged in a single plane.

The most conspicuous character of difference is undoubtedly the form of the mature inflorescence: lax and with drooping branches in *P. mauritianus* (fig. 1); more compact with straight or only very slightly drooping branches in *P. australis* (fig. 2). (The photograph reproduced in Chippindall, 1955: 228 is almost certainly of *P. mauritianus*). Clayton, 1967, referred to these inflorescence differences in his key as follows: "... panicle often smaller, the lowest node usually few-branched, some of the branches bearing spikelets nearly to their base ..." (*P. australis*); "... lowest node of the panicle often many-branched in a whorl, the branches bare of spikelets for some distance from their base" (*P. mauritianus* and *P. karka*). The disposition of the spikelets on the branches largely governs the lax, or compact, appearance of the whole inflorescence, which character can be observed some distance from the population, and therefore serves as a valuable first clue to identification. Some provisos are necessary, however. With ageing, the several florets of each spikelet are shed, leaving the glumes persistent upon the inflorescence branches. Panicles of both species, at this stage, look considerably less compact than do the same panicles when many florets are undergoing anthesis. Within a population, flowering of plants is usually simultaneous, nevertheless some younger and some older inflorescences are always represented among a majority at peak of development. Thus representatives of similar age should be compared. In *P. australis* the uppermost culm leaf frequently sheaths the base of the panicle: this emphasizes the impression of its compactness and makes dissection necessary to see the arrangement of the lowest inflorescence branches. In both species, two nodes separated by only a short internode often mark the inflorescence base. Each node carries usually a single branch that is itself branched from almost the extreme base. The close proximity of the two nodes suggests a whorled arrangement that is not actually represented, so that Clayton's criterion of panicle branching often does not hold in South African specimens of *P. mauritianus.*

With emergence of the immature inflorescence and during subsequent flowering and fruiting, leaves dry and fall away progressively from the base of the culm upwards. The position of the abscission layer responsible for this loss provides another distinguishing character useful in the field. In *P. mauritianus* it develops in the leaf sheath immediately above the node from which the leaf arises, so that leaf sheath and blade are shed as a unit, leaving the internode bare with the axillary bud exposed (fig. 3). In *P. australis*, abscission takes place at the base of the leaf blade immediately above the collar, so that the blade falls leaving the sheath enveloping the stem and generally overlapping the internode and sheath above (fig. 4). This sheath has to be artificially removed before the axillary bud becomes visible. By time inflorescences are mature, flowering stems may have lost all but the uppermost six to five blades, but internodes, in the basal two-thirds, are clothed in persistent leaf sheaths. In *P. mauritianus*, by contrast, culms bearing mature inflorescences usually carry more than six leaf blades, but consist of naked internodes (often pinkish or purplish if habitat conditions are more extreme than usual) with lateral buds exposed in the middle region, the base bearing bract-like scale leaves only

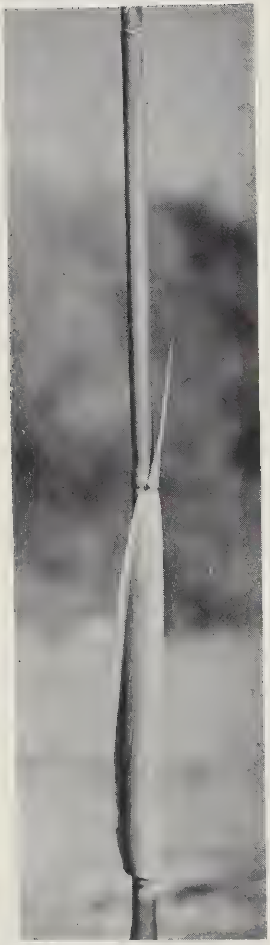

FIG. 3.

Phragmites mauritianus: portion of flowering stem showing, below, leaf sheath abscising immediately above node; above, axillary bud exposed by leaf sheath already fallen.

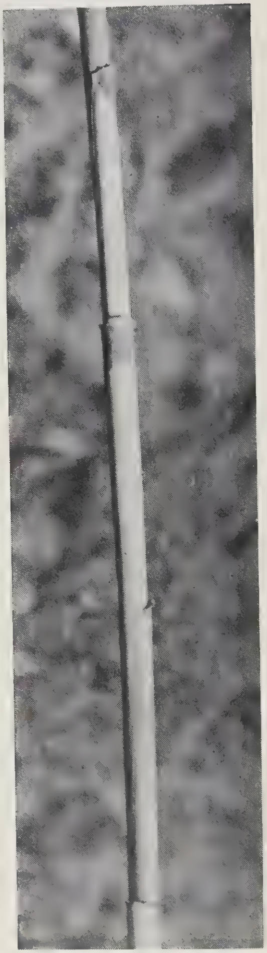

FIG. 4.

Phragmites australis: portion of flowering stem showing overlapping persistent leaf sheaths: leaf blades already fallen as a result of an abscission layer developed at the junction of each blade with its sheath.

little better developed than are those of the rhizome. In *P. australis* the leaf blades persisting below the inflorescence frequently lie in a single plane (visible in fig. 2: culm on left) whereas this seldom if ever applies in *P. mauritianus*.

After flowering, culms of *P. australis* die back either to ground level or to the first side branches, if such are present, but expansion of the lateral buds in this species is unusual (a statement supported by Haslam, 1969a: 128; 1969b: 289) and seems attendant upon breakage or damage of the stem apex. In *P. mauritianus* the previous summer's flowering stems die back the following spring, but distally only, so that the major part of each culm remains photosynthetically active. These differences in growth pattern afford another means of distinguishing between the species in the field, for the complete die-back of usually unbranched stems in *P. australis* contrasts with die-back of the distal tips only of usually well branched flowering stems in *P. mauritianus*. Thus where populations have not been subjected to fire in the post-flowering period of winter to early spring (firing is a frequent happening in Natal), dead culms among densely produced new lateral innovations are a feature of populations of *P. australis*, but are lacking in *P. mauritianus*. Caution must be observed, however, for without careful scrutiny to detect evidence of firing, use of this single criterion as a means of species distinction can be misleading.

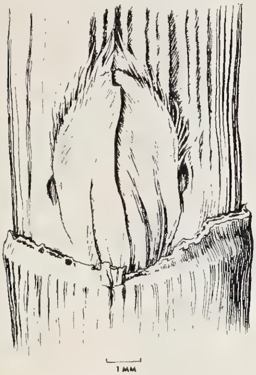

FIG. 5.
Phragmites mauritianus: axillary bud.

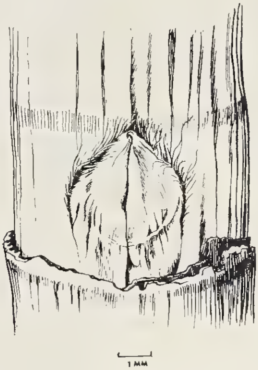

FIG. 6.
Phragmites australis: axillary bud.

The dormant axillary buds, themselves, differ in form (figs. 5, 6): the differences appear constant but are difficult to express accurately in words. Buds of *P. australis* are more markedly recessed into the nodal tissue than is the case with *P. mauritianus*, and are more nearly round in outline in face view

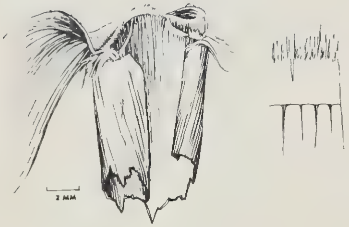

FIG. 7.
Phragmites mauritianus: left: apex of leaf sheath and base of blade showing ligule and tufts of fine white hairs on either side near sheath mouth (erect hairs behind ligule lacking); right: portion of ligule, in detail.

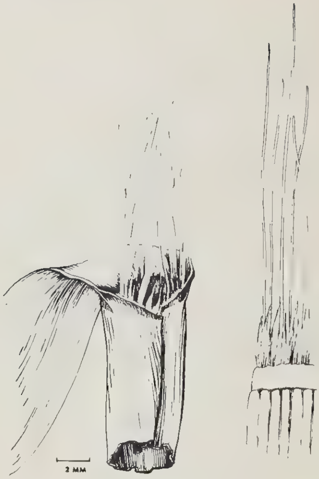

FIG. 8.
Phragmites australis: left: apex of leaf sheath and base of blade showing ligule and erect white hairs arising from behind ligule; right: portion of ligule with erect white hairs behind, in detail.

with a definite basal pediment that is absent in the more oval, usually larger buds of *P. mauritianus* (culms of approximately the same diameter should be compared). Outermost protective bud sheaths in both species are hairy marginally in the upper half, but hairs in *P. mauritianus* are more numerous and form a thicker, more conspicuous fringe. Another useful difference detectable in the field, lies in features of the ligule. In *P. australis* leaves near the apices of actively growing sterile shoots show well the long, erect, white hairs produced immediately behind the ligule. These are especially conspicuous when the leaf blade is folded back. In *P. mauritianus*, such hairs are usually either shorter, fewer and finer, or occasionally may be absent (figs. 7, 8, 9), and are always accompanied by shorter, finer more bunched trichomes at either side of the sheath mouth, in the position where auricles sometimes occur in other grasses. The long hairs behind the ligule in *P. australis* dry with age and break or fall away, as eventually do the shorter ones of *P. mauritianus*. Old leaves, or leaves below an inflorescence thus should not be examined for characters of the ligule.

Differences in leaf blade colour, texture and apex exist in the two species. These are usually clearly evident in Natal populations, especially when both taxa grow in fairly close proximity and can be compared in the field. Blades of *P. australis* are glaucous blue beside the yellowish green of *P. mauritianus;* soft against the stiffer harder texture of the latter; they wilt and roll rapidly when detached, suggesting either greater water loss in a given time, or less ability to withstand equal loss without permanent damage; apices are far more gradually tapering and much longer acuminate in *P. australis* than in *P. mauritianus*, while reduced blades of the developing axillary shoots have soft apices in the former, but are pungent and penetrating in the latter. (Clayton, 1967: 115 also observed differences in leaf blade apex in the two species, expressing them as follows in his key "leaf blades . . . the tips filiform and flexuous . . . *P. australis*. Leaf blades . . . the tips attenuate, stiff or even pungent . . . *P. mauritianus*.") While these differences apply in Natal and further north where environments are sub-tropical, they are not as readily detectable in plants of the winter rainfall area of the south-western Cape Province. Firstly, it should be recalled that no natural stands of *P. mauritianus* are presently recorded for the

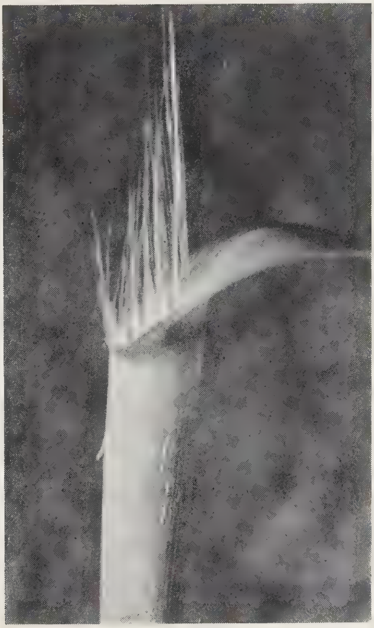

FIG. 9.
Phragmites australis: portion of leaf sheath from sterile aerial stem with leaf blade folded back to show erect white hairs.

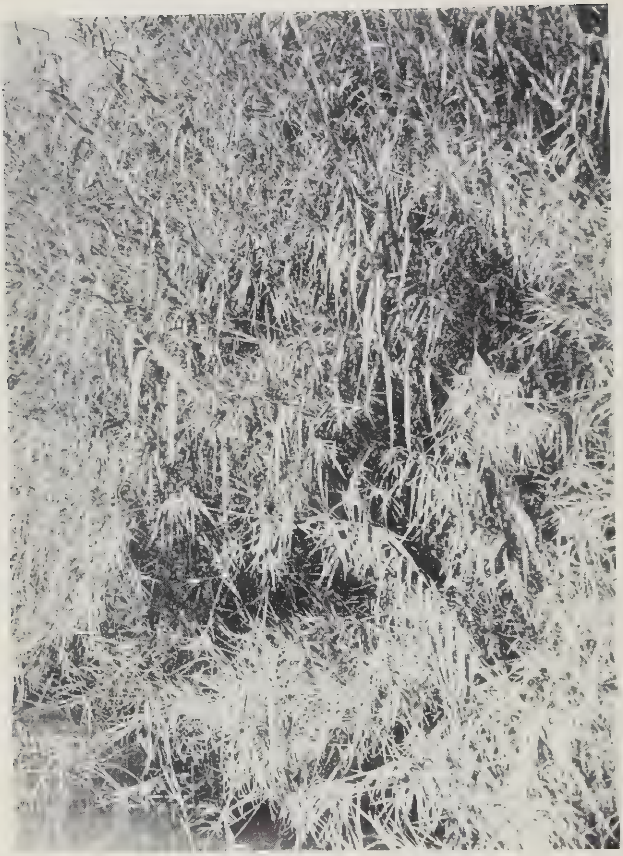

FIG. 10.
Phragmites mauritianus: portion of population fringing Umgeni River at Morton's Drift, showing profuse branching of aerial stems.

Cape Province, so that populations of both species growing under conditions of winter rainfall are not available for comparison. Secondly, the dry summer season seems to produce (under certain ecological conditions of intermittent water supply at least), greener rather than more bluish leaves in *P. australis* and more effectively pungent reduced leaf blades to axillary shoots than is the case at less southerly latitudes. There are possibly other habitat factors that may result in the development of sharper, firmer apices to leaves of axillary shoots in *P. australis* (see Haslam 1969c: 707 with reference to salinity). Further field observation of *P. australis* in the Cape Peninsula and in arid South West Africa is needed.

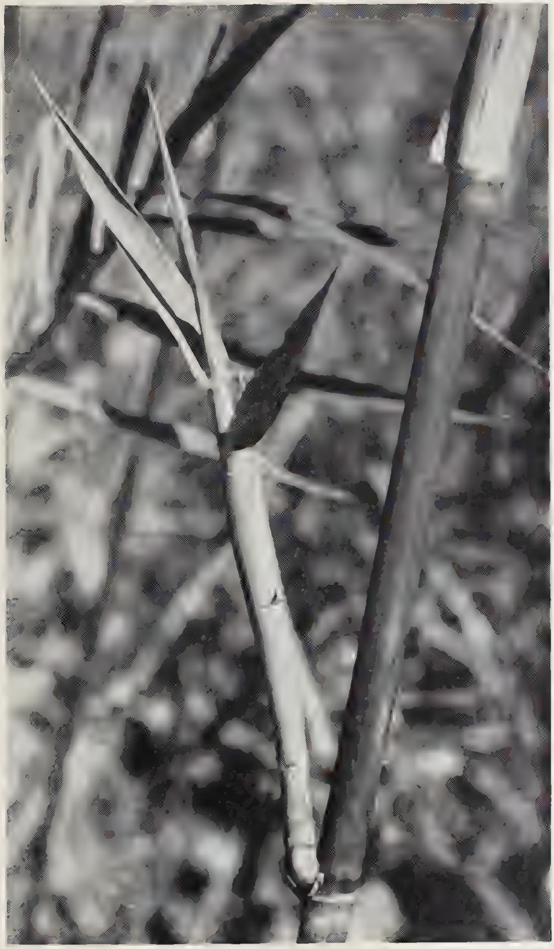

Fig. 11.

Phragmites mauritianus: expanded axillary shoot showing pungent apices to leaf blades and tufts of fine white hairs at sheath mouth.

Haslam (1969a) in studying *P. australis* = [*P. communis*] in the British Isles and Malta, recognized the occurrence of four different stem types in this plant, namely, horizontal rhizomes (the juvenile type responsible for renewing the stand), vertical rhizomes (which bear aerial shoots), aerial shoots (the photosynthetic, potentially flowering, short lived stems) and legehalme (the non-rigid runners of indefinite growth produced most commonly in new communities or in brackish water). All four stem types are represented in Natal plants of *P. australis*. It is the mature stem type, the aerial, short-lived, photosynthetic, potentially flowering stem that has been dealt with in this paper up to now. Legehalme were commonly produced when plants were colonizing newly developed mud banks (Ward 6597), occasionally developed in populations growing in brackish water (Ward 6594: 6598). Lengths for legehalme exceeding eleven metres were measured, which agrees with Haslam (1969a: 129), who reports their lengths as greater than those of any other stem type, "... frequently reaching 10 m". In other respects, too, the legehalme of Natal plants of *P. australis* agree with those described by Haslam for plants of the northern hemisphere.

The white, horizontal rhizomes are generally dorso-ventrally flattened;

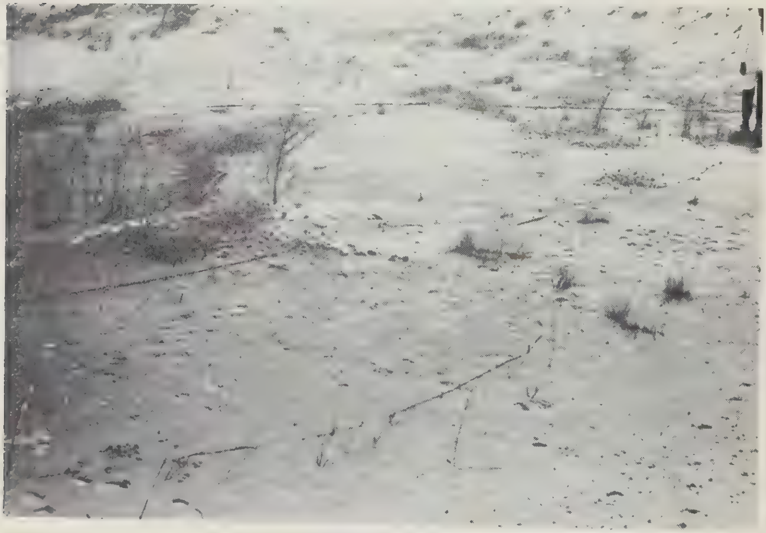

FIG. 12.

Phragmites australis: legehalme developed where plants are establishing themselves on clayey mud: Durban Bayhead, June, 1970.

sometimes they flex above ground level to form a photosynthetic knee (Ward: 6764). Adventitious roots radiate in all directions from subterranean nodes, but only descend from nodes on or close to the soil surface.

In *P. mauritianus*, legehalme have never been observed, but the other stem types are the same as in *P. australis*, except that type for type and branch sequence for branch sequence they are more robust.

In the Natal populations of both species studied in detail, young inflorescences became evident above the apical culm leaves in December. Anthesis was at varying times from March to July, mainly April to June inclusive, while fruit was dispersed (in *P. australis*) over the period April to July inclusive. In *P. mauritianus* heads were apparently fruiting from (March) April-June (July), but whether viable seed was actually dispersed is open to question since laboratory study of representative heads yielded no perfectly formed mature fruits.

3. *Results of Ecological Study*. No more than observational notes and suggestions for further study are given here, for it was not possible to undertake experimental investigation into the habitat conditions favoured by each species.

From observation it became apparent that the two species have different habitat requirements. This is of particular interest, since, in Natal at any rate, populations of each species are often to be found in the same general locality. Sometimes this is the case inland: frequently it is so at the coast where populations may occur juxtaposed, or almost so, or where plants of *P. mauritianus* may surround, or partially surround, or penetrate as local minor intrusions, extensive stands of *P. australis* that are otherwise pure.

P. australis grows in swamps or vleis, or in other places with restricted drainage such as river back-waters more or less isolated from the main stream, or in standing water up to 70 cm deep, often forming extensive reed swamps. Plants extend into inter-tidal estuarine areas, especially where the salinity is reduced by the inflow of fresh water. (Measurements of salinity, from $0{\cdot}3\%$ after heavy rains, to $2{\cdot}1\%$ after neap tides and $3{\cdot}1\%$ after spring tides, were recorded for Isipingo populations during the present study using the specific gravity method. High salinities were usually not of long duration, however.) The soils favoured were generally moist organically rich sand, or clayey sand and mud. Occasionally plants occupy steep mesoclinal banks where there is no visible water: here the soils are always clayey rather than sandy.

P. mauritianus, on the other hand, occurs in riverine situations, often flood plains preferably with well-drained, often sandy soils and permanently flowing or frequently moving water, or in other moist situations especially where there has been recent disturbance of the habitat. The horizontal rhizomes readily penetrate sandy alluvial deposits, so that plants are often the first perennials to re-colonize flood disturbed river banks. Only rarely does the species extend to where plants may be affected by the extreme high water of an equinoctial spring tide. Frequently local populations grow well away from visible or near surface water. Such situations may be north or east-facing and thus more xeric than those favoured by *P. australis*, with soils sandy rather than clayey.

Where plants of *P. mauritianus* partially surrounded, or extended as local penetrations into, populations of *P. australis*, investigation showed disturbance of the habitat originally occupied by *P. australis* in the areas invaded (particularly in respect of soil/water relationships), thus affording suitable conditions for colonization by *P. mauritianus*. Such disturbance was either due to the deposition of soil by flooding or was the outcome of man's activities. In one case, at Isipingo, the only penetration into a population of *P. australis* by *P. mauritianus* was where a drainage exit from the swamp had been constructed. Where disturbance resulted in impeded drainage or the deposition of clay soils, *P. australis* was occasionally found to have re-established itself. Thus in localities where both species are represented, it is edaphic conditions that seem to control the patterns of distribution. It is at present no more than speculation to suggest that oxygen levels within the soil and water of the habitat may be limiting in determining where *P. mauritianus* can survive. Certainly this species seems to require better drainage, and thus aeration of the substrate, than does *P. australis*. It also seems better able to withstand drier conditions, but this may apply only under sub-tropical conditions, for in the south western Cape during the dry summer months, *P. australis* may be seen flourishing in dry (at least superficially so) water courses.

Because of these different habitat requirements, the distributional pattern of the two species is frequently revealing in gaining understanding of the pattern of environmental change within an area. Particularly is this so along the coast and along some river courses where isolated relict patches of *P. australis* indicate the earlier presence of extensive reed swamps or poorly drained vlei areas. At Midmar Dam, in April, 1968, below the sluice-gates of the main dam wall a portion of a population of *P. australis* was still standing in what had been a vlei area. Slightly below this, evidence of the dumping of large mounds of soil into this vlei was still apparent. Much of the dumped soil had already been colonized by *P. mauritianus* which was flowering, as was *P. australis*. With disturbance of the habitat, evidence suggests that plants of one, or other, species may eventually disappear leaving little, if any, evidence of previous prevailing conditions. Nothing definite is known of the time that might be involved for such changes to be completed, however.

Physio-ecological water relationships of intact plants of each species may repay investigation. The inter-play, if any, between pattern of leaf abscission, rate of water loss from the plant as a whole unit, and survival within a particular type of habitat, especially where seasonal fluctuation in water levels occurs, are not understood. It may be that plants of *P. australis* with their habit of leaf blade abscission and complete die-back of post-flowering culms are less demanding of available water during the winter season than are plants of *P. mauritianus* in which post-flowering stems remain leafy and thus active transpirationally. On the other hand, the harder leaves of the latter may, perhaps, transpire less water than those of the former, and thus be hardly more demanding of available water during the unfavourable season than the non-leafy stems of *P. australis.*

In plants of *P. australis* growing where saline conditions prevailed and where the habitat had been infilled with sandy clay (Ward 6763), adventitious roots developed from the horizontal rhizome were greatly swollen, obviously serving a water storage function. Such markedly swollen roots have not been found in other habitats, nor yet at all in *P. mauritianus*, but it may be that the adventitious roots do serve as a useful water reserve in certain environments.

Haslam (1969a, b and c) has drawn attention to aspects of ecological behaviour in plants of *P. australis* growing in northern latitudes that are of some significance in southern populations and which may well operate within plants of *P. mauritianus* also.

This author has shown the growth pattern for northern populations of the former species to be as follows. Underground horizontal rhizomes grow during autumn. As a result of internal control, each changes into a vertical rhizome which, when internal dormancy ceases and provided the external environment is generally favourable, develops in spring into an erect, aerial, photosynthetic, potentially flowering stem. On all parts of this system, axillary buds are produced one at a node. On horizontal and vertical rhizomes, buds may be laid down almost all the year round, but remain underground while internal dormancy operates. This ceases in spring, when, provided temperatures are not too low and thus in turn limiting, the buds emerge to develop into aerial stems. The period of emergence is relatively rapid and once begun continues without re-establishment of internal dormancy even if low temperatures again obtain. Emerged buds and aerial stems are frost sensitive, whereas underground rhizomes and legehalme are not.

Fire, provided sufficiently severe to sever the aerial stems, breaks internal dormancy, and bud emergence, provided environmental temperatures are not too low, commences about a month after firing. Severe fires which scorch the ground may delay bud emergence for two months, possibly because of direct influence on the rhizomes. Cutting of rhizomes also causes breakage of internal dormancy, thus such treatment (ploughing) may hasten bud emergence. Cutting of aerial, photosynthetic stems late in the growing season has little effect on the population, but early in this season such treatment prevents the laying down of adequate food reserves and thus depletes subsequent growth. Haslam states that early spring/summer cutting of photosynthetic stems is consequently the best (simple) means of controlling northern populations of *P. australis*.

The general growth pattern in southern populations of both species is the same as determined by Haslam. Because of sub-tropical maritime climates, the coastal southern African populations in particular, as far south as the western Cape, will be little influenced by frost, but cold may well have an effect in delaying emergence of aerial shoots in inland populations, especially those near the mountains. Fire is another factor which undoubtedly influences almost all southern African populations either regularly or occasionally (with the possible exception of South West African stands). In Natal, a dense coverage of aerial shoots emerges after firing, but the time lapses between firing and visible growth of young emerging shoots for individual populations were not precisely noted.

Haslam also mentions the adverse effect on emergence of aerial shoots of lack of flooding and dry environmental conditions, and of salinity upon intercalary growth, which influences internodal length producing shorter stems. Leaves, under these conditions, tend to be more markedly xeromorphic (more pungent apically). Ranwell and co-workers 1964: 637 concluded from work done in southern England that mature plants of *Phragmites* could not survive where the soil solution at 10 cm depth exceeded 1·2% chlorinity (2·0% salinity), (presumably for any length of time—our proviso). All these points should be kept in mind when considering southern populations particularly in relation to damming, siltation, and changes in estuarine environments that may be the direct or indirect outcome of natural or man-influenced environmental change.

B: *In the Laboratory*

1. *Spikelet Morphology*. Clayton's (1967) work and comments formed the basis of a preliminary survey carried out to determine features of spikelet structure likely to prove most reliable and easy to use in helping to distinguish between *P. australis* and *P. mauritianus* in South Africa. Lengths and widths of glumes and first (lowest) lemma seemed most promising, with number of florets to the spikelet affording another possible criterion not previously in use. No other features of the spikelet that had not already been considered by other workers warrented assessment.

With these guiding ideas in mind, field samples were studied, each group of approximately fifteen flowering stems (fewer in the case of Umbogintwini) being regarded as representative of a population and providing thirty spikelets taken at "random" for scoring.

Despite the greater number of florets often present in spikelets of *P. australis*, it soon became apparent that this parameter could not be included among re-

TABLE 1
Populations of *Phragmites mauritianus* studied in detail

Code	Grid Ref. & Specific Locality	Collector's Name & No.	Habitat Conditions
Peattie's Lake	Natal—2930 (Pietermaritzburg): Umgeni Valley (-AD): small streamlet to north of Peattie's Lake	Gordon-Gray, K.D. 6158	in clayey mud of bank and in moving water, up to c. 1 m in depth, of streamlet.
Morton's Drift	Natal—2930 (Pietermaritzburg): Umgeni river: Morton's Drift (-AD) near Otto's Bluff	Gordon-Gray, K.D. 6157	in clayey mud, among dolerite boulders of bank and in moving water of Umgeni river.
Albert Falls	Natal—2930 (Pietermaritzburg): Umgeni river near Albert Falls (-AD)	Gordon-Gray, K.D. 6159	in dry grassveld: fairly low-lying: inundated under flood conditions.
Midmar	Natal—2930 (Pietermaritzburg): Umgeni river, Midmar Dam: (-CA) immediately downstream of main dam wall	Gordon-Gray, K.D. 6160	in doleritic soil of infill into vlei originally occupied by *P. australis:* plants c. 2 m above river level.
Mpushini Valley	Natal—2930 (Pietermaritzburg): Ashburton, Mpushini Valley (-CB) 29°40′S 30°28′E	Ward 6586	in clayey loam (ex dwyka tillite) on floor of small, dried dam c. 2,000 ft.
Mlazi River	Natal—2930 (Pietermaritzburg): Mlazi River: (-CD) on main road between Eston & Umlaas Rd. 29°46′S 30°31′E	Ward 6587	in alluvial loamy clay on and between boulders at side of river from 1·2 m above current water level to wet clay at river's edge.
Hammarsdale	Natal—2930 (Pietermaritzburg): Hammarsdale (-DA) off main Durban-Pietermaritzburg road	Gordon-Gray, K.D. 6155	in sandy dry soil on hillslope above small streamlet (no water visible)
Isipingo	Natal—2930 (Pietermaritzburg): Isipingo (-DD) 29°59′S 30°57′E	Ward 6584	in moist silty sand alluvium on bank of upper estuary, above tidal range except at spring tide when bases covered at high water c. 1 m alt.
Isipingo Flats	Natal—2930 (Pietermaritzburg): Isipingo Flats (-DD) 29°59′S 30°56′E	Ward 6590	in alluvial, slightly silty sand in former flood diversion canal c. 2 m alt.
Karridene	Natal—3030 (Port Shepstone): Mzimbazi Valley, W. of Karridene (-BB) 30°07′S 30°49′E	Ward 6593	in alluvial sand on floodplain of stream, in thicket. c. 4·5 m alt.

TABLE 2
Populations of *Phragmites australis* studied in detail

Code	Grid Ref. & Specific Locality	Collector's Name & No.	Habitat Conditions
Estcourt	Natal—2929 (Underberg): Estcourt (-BB) beyond township on road to Tabamhlope	Gordon-Gray K.D. 6279	in fine alluvial mud: low-lying flat area (no water visible, but water would stand after rain): c. 100 m from streamlet in grassveld.
Cedara	Natal—2930 (Pietermaritzburg): near Cedara College (-CB) stream between main road and railway	Gordon-Gray, K.D. 6282	in alluvial mud: flat area extending beyond banks of streamlet: plants in standing water.
Eston	Natal—2930 (Pietermaritzburg): Eston (-DC): junction of road D 362 with main Eston-Umlaas Rd.	Ward 6588	wet clay of swamp: low-lying flat area on both sides of water course in flat valley—c. 670 m alt.
Bluff	Natal—2930 (Pietermaritzburg): Durban Bluff (-DD) on flats on road to Wentworth Hospital	Gordon-Gray, K.D. 6156	in sandy soil: flat low-lying area (no water visible, but water would stand after rain): c. 1-2 m alt.
Isipingo Flats	Natal—2930 (Pietermaritzburg): Isipingo Flats (-DD) 29°58′S 30°56′E	Ward 6589	in red sandy soil of built-up road bank, plants growing through infill from former swamp: originally in clayey, fine sandy silt on alluvial plain.
Isipingo Beach	Natal—2930 (Pietermaritzburg): Isipingo Beach (-DD) 29°59′S 30°56′E	Ward 6597	in bush-cleared and levelled low-lying area in alluvial sand with humus and in clayey sand infill: c. 1 m alt.
Umbogintwini	Natal—3030 (Port Shepstone): Umbogintwini Lagoon (-BB) extremity of Golf Course 30°00′S 30°56′E	Ward 6596	in moist, alluvial silty loam, in depression on floodplain of upper estuarine lagoon, recently shallowly inundated: c. 1 m alt.
Umtamvuna	Natal—3130 (Port Edward): Umtamvuna river (-AA) 31°04′S 30°11′E	Ward 6755	in sand and mud at edge of estuary extending into water: c. 1·5 m alt.
Mzamba	Transkei—3130 (Port Edward): Pondoland, Mzamba (-AA) 31°06′S 30°10′E	Ward 6747	in beach sand at edge of estuary: c. 3 m alt.
Haven	Transkei — 3228 (Butterworth): mouth of Bashee River (-BD)	Gordon-Gray J.L. 862	in sand and mud under estuarine conditions, extending into water.

Table 3

Phragmites mauritianus and *P. australis:* some spikelet parameters of populations sampled in the field (figures derived from 30 spikelets from each population listed in tables 1 and 2)

	P. mauritianus (for 300 spikelets)	*P. australis* (for 300 spikelets)
Lower glume length in mm:		
extremes	2·0—4·8	3·1—7·0
mode	3·0	5·0
mean	3·3	4·8
Upper glume length in mm:		
extremes	3·0—5·7	5·0—9·2
mode	4·0	7·0
mean	4·2	7·0
First (lowest) lemma length in mm:		
extremes	4·7—10·0	7·5—15·0
mode	8·0	11·0
mean	7·3	11·3
Sum of lengths of lower and upper glume and lowest lemma in mm	10·2—19·7	18·3—27·0

liable indicator characters by which to distinguish the species. Firstly, there is overlap in floret number per spikelet: secondly, fragmentation of the rachilla from the apex downwards commences soon after anthesis of florets and is rapid after drying out, so that only comparatively young inflorescences showed full number of florets.

Measurement of glumes and first lemma revealed that ratios of width to length of these organs showed overlap between the taxa. Lengths also showed overlap, this being minimal in the case of the upper glume. When lengths for these three organs were summed for individual spikelets, the overlap persisted but was slight. This parameter and upper glume length were thus regarded as the most convincing spikelet characters by which to distinguish the taxa, especially when working with herbarium specimens.

Extremes, modes and means for lower and upper glume length and first (lowest) lemma length for thirty spikelets from each of the twenty populations listed in tables 1 and 2 were recorded. Since results were remarkably uniform and showed no significant variation in relation to habitat or locality, only the extremes, modes and means for all 300 spikelets measured within each species are given in table 3. (Figures for individual populations are available from one of the authors, KDGG, should they be required.) To gain evidence of variation in size of spikelet parts within populations distributed over the remainder of the sub-continent, parameters for thirty spikelets within each species, each spikelet taken from an herbarium sheet from a different locality, were measured.

Extreme lengths for these samples were well within extremes recorded for Natal populations.

Clayton (1967 and 1968) recognized within *P. australis*, subsp. *australis* from temperate regions of both hemispheres (thus including S. Africa), and subsp. *altissimus* for the large Mediterranean form. The latter, apart from its greater height and larger panicles, was distinguished (albeit "... rather imperfectly ...", as the author himself states) on upper glume shape and apex. Clayton also mentioned that the few tropical American specimens he had examined also appeared to fit this subspecies. Some S. African populations (Ward, Isipingo 6574 and Isipingo Flats 6589), as well as some herbarium specimens, particularly from the Cape Province and Orange Free State (for example Paterson 1043 BOL; Steyn 49 NBG) fit the glume requirements for this variety.

In view of the possibility that Clayton's subspecies is also S. African and thus not geographically separate from subsp. *australis*, no emphasis is placed on intra-specific categories.

2. *Leaf Anatomy*. Metcalfe (1960) urged caution in the placing of too great emphasis upon differences in leaf anatomy in the identification of closely allied species. No reminder of the close relationship between *P. mauritianus* and *P. australis* is necessary, so the differences in the anatomy of their leaf laminae, as seen in transverse sections and in the abaxial epidermides, are given with this warning in mind. The details may, nevertheless, assist those who are occasionally called upon to identify sparse, dry, leaf fragments or field populations not yet in flower: they may perhaps help, too, by adding to overall knowledge of anatomical variation in one of the world's most widely distributed angiosperms (*P. australis*), and in further elucidating relationship of the phragmitiform grasses within Gramineae, a problem that as yet has not been conclusively resolved.

Leaves from the twenty populations studied in the field were sectioned and epidermal tissues stripped. Mature leaves of approximately the same age were used (usually the fourth leaf from the apex of a sterile stem: only fertile stems were available for Umbogintwini). Preparations were made from midway along each blade. Staining was uniform for preparations of the same type.

T. S. Lamina. All laminae sectioned showed agreement in main structural features with Metcalfe's (1960: 385) description for [*P. communis*] = *P. australis*, so this account is taken as standard for both species. The keel, which in the S. African leaves of both species, was far less well developed with less parenchyma between abaxial vascular bundles and adaxial epidermis than in the illustration referred to for *P. australis* (Metcalfe, l.c. fig. XIII, 3), was the most striking point of difference.

The several layers of palisade cells on the abaxial side of the leaf described for *P. australis*, were well defined in laminae of *P. mauritianus* also: in addition rather well defined palisade cells occurred adaxially as a rule. Metcalfe did not mention invaginated walls in any of the mesophyll cells, but in South African specimens these were well defined, especially in *P. mauritianus*, in fairly large cells situated between the abaxial epidermis and the bulliform cells. If these are arm cells, recorded so far only for Bamboos and members of Oryzeae (and there seems no immediate reason why they should not be so regarded), do they reflect closer relationship between *Phragmites* and the Bambuseae and Oryzeae than is presently considered probable?

Early study suggested that differences in number of vascular bundles between each pair of larger ones, outline shape of the small bundles (parenchymatous outer sheath included), and number of cells comprising this sheath, might be consistent for each species and might thus provide additional characters of distinction between them, but examination of all representative populations showed overlapping ranges of variation. The straightness of ad- and ab-axial surfaces in *P. mauritianus*, did, however, contrast consistently with the shallow ribs and furrows of comparable surfaces in *P. australis*. Extremes in some characters of lamina anatomy are illustrated in plan in fig. 13 a, b, and in detail in figs. 14, 15 but, as has been stated there is a range in each taxon resulting in overlap between these extremes.

Abaxial Epidermis. Metcalfe's (1960: 385) description for *P. australis* was valid for South African plants, except that walls of the long cells between the veins were thick and pitted rather than thin, a feature even better developed in *P. mauritianus* (fig. 16a).

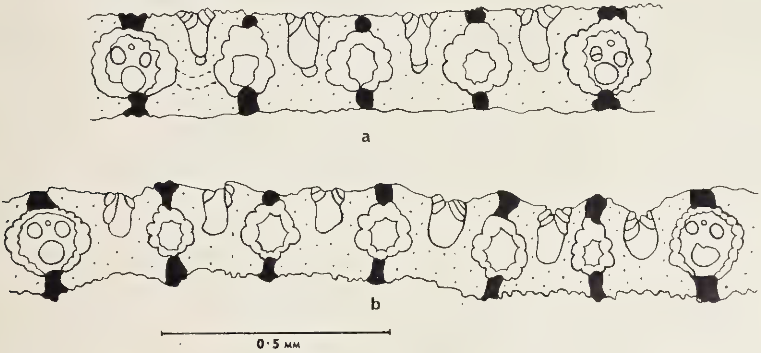

FIG. 13.
Anatomy of leaf blade in plan: a. *P. mauritianus;* b. *P. australis.*

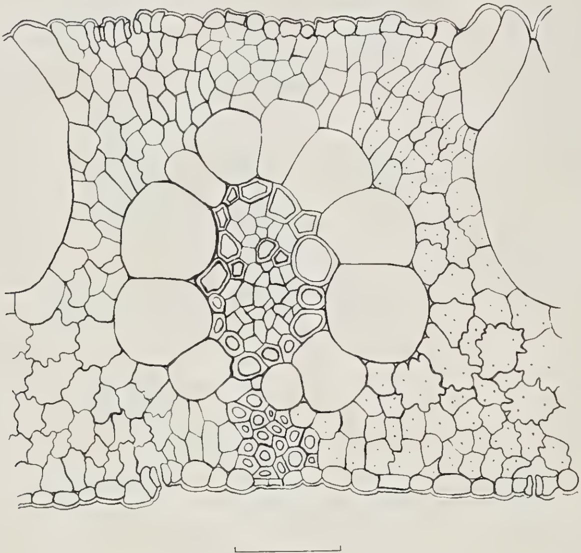

FIG. 14.
Phragmites mauritianus: portion of leaf blade in detail.

Apart from differences in disposition of the short cells in the stomatal bands (a cork and a silicified cell paired in *P. australis;* often only a solitary silicified cell in *P. mauritianus*), distinctions in abaxial epidermal structure between the taxa lay in the nature and disposition of the dermal appendages. Micro-hairs (fig. 16b) were readily detected on all leaves of *P. mauritianus* studied, being situated in those parts of the intercostal zones lying between the stomatal bands and the veins, and occasionally in the stomatal bands, but were *never* seen on leaves of *P. australis* as Metcalfe (1.c) also reports. This difference might not be meaningful in species diagnosis, in the light of variation observed for *Cortaderia selloana* by Metcalfe and Clifford (1968: 490), but it is certainly of interest in regard to the taxonomic relationship of the phragmitiform grasses within Gramineae. Leaves of *P. mauritianus* bore rows of prickle hairs as out-growths from epidermal cells above the veins. These sometimes varied markedly in size from one vein to the next on the same leaf, the largest bearing elongate, pointed apices almost the length of the cell itself (Isipingo Flats; Mlazi). No prickle hairs were seen on leaves of *P. australis*, but over the veins unpointed prickles of the type illustrated for *Arundo donax*

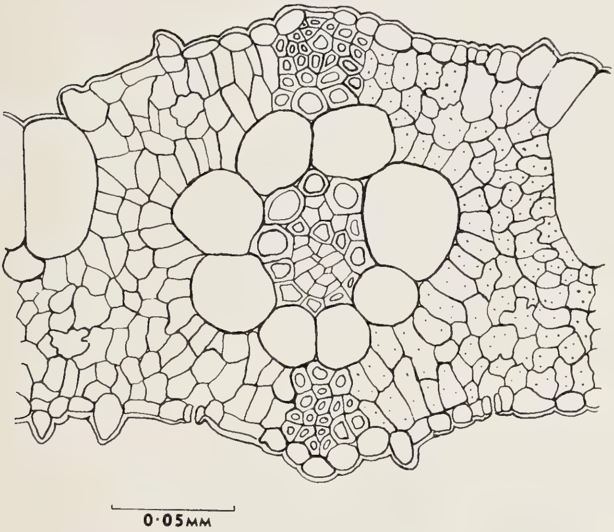

FIG. 15.
Phragmites australis: portion of leaf blade in detail.

(Metcalfe, 1960: fig. VI, 6) were frequent and somewhat variable in size, but much more uniform in dimensions than were the prickle hairs of *P. mauritianus*. On leaves of *P. australis* hooks were frequent in the intercostal zones, commonest among the stomata, almost invariably paired with a cork cell, but occasional also between the stomatal bands and the veins. On leaves of *P. mauritianus* hooks were occasional in the last named position, but almost, or entirely, absent from among the stomata.

Adaxial Epidermis. The only point worthy of note was that microhairs and prickles occurred at intervals fringing the rows of slightly sunken bulliform cells in *P. mauritianus*, whereas only hooks were found in this position on leaves of *P. australis*.

3. *Chromosome Number.* Counts of somatic chromosomes carried out on tissue of young axillary shoots developed on aerial stems gave n = 48 for *P. mauritianus* (two populations counted, Pietermaritzburg and Hammarsdale) and n = c. 96 for *P. australis* (two populations counted, Durban and Karridene).

Avdulov (1931) (see Darlington and Wylie, 1961) cited both these numbers for *P. communis*, as did Bor, 1960: 416 for *P. communis* var. *communis* in India.

From the literature no record of chromosome number for plants identified as *P. mauritianus* could be traced. Can it be that material of this species was included among that of *P. communis* when counts were made, as in the past the distinction between them was not always recognized? This is no explanation for Bor's counts, since *P. mauritianus* is not recorded for India.

When time permits, further counts on Natal and South African populations must be carried out to determine the full range of somatic numbers represented. The populations investigated so far are not ideally representative in that both within *P. australis* were coastal, both within *P. mauritianus* were from further inland. For the genus *Phragmites*, however, it seems reasonably conclusive that x = 12 or 6. (Bews 1929 cites Tischler, 1927 as recording 2n = 18 for [*P. vulgaris*] = *P. australis:* see also Stebbins, 1958: 171.)

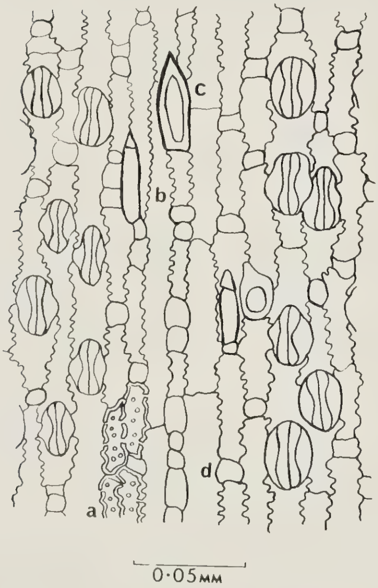

FIG. 16.
Phragmites mauritianus: portion of abaxial epidermis of leaf blade:
a. long cells showing thick, pitted walls.
b. microhair. c. prickle hair. d. silica cell.

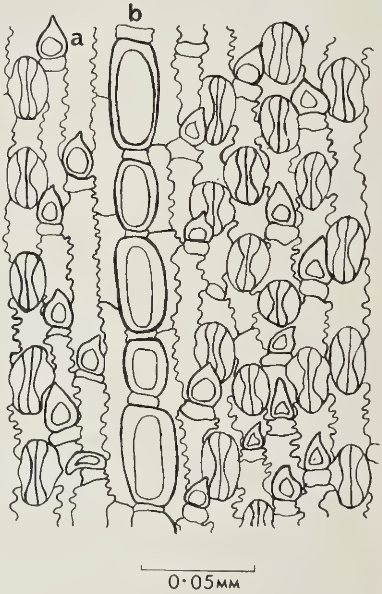

FIG. 17.
Phragmites australis: portion of abaxial epidermis of leaf blade:
a. hook paired with cork cell. b. unpointed prickles in portion of row of cells over vein.

DISTRIBUTION

Present distributional records have been based on plants collected by both authors, and on herbarium specimens named against presently recorded differences between the taxa. In how far known records really express the situation in nature is questionable: the reasons for this are two-fold. Firstly, *P. mauritianus*, growing as it does where there has been some disturbance of the habitat, and often where conditions are drier, may partly or completely fringe populations of *P. australis*. Thus plants of one taxon may have been first to the hand of the collector, who unaware of differences between the species, may have failed to record the presence of both. Secondly, the ubiquitous presence of *Phragmites* wherever the authors have travelled since commencing this survey (thus becoming conditioned to looking for plants), has suggested that the genus is more widespread throughout the sub-continent than records show.

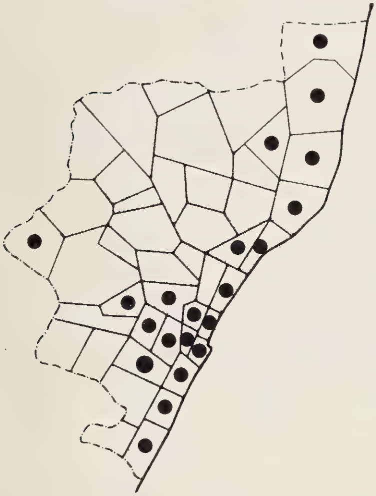

FIG. 18A.
Phragmites mauritianus: map showing known distribution in Natal.

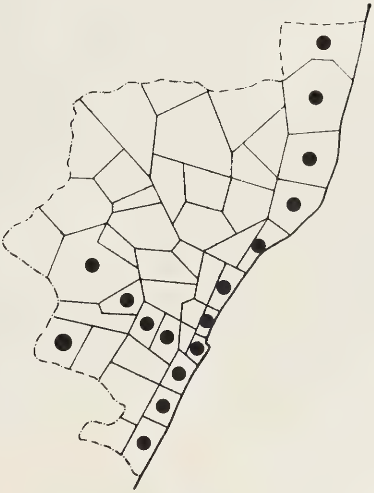

FIG. 18B.
Phragmites australis: map showing known distribution in Natal.

Note: in the above maps one dot has been placed centrally in each magisterial district from which the species is known.

NATAL. The known distribution in Natal of *P. mauritianus* and *P. australis* is shown in figs. 18a and 18b respectively. Both taxa are especially well represented along the coast. Ward 6757 from the Mpenjathi river, approximately

16,000 m (10 miles) north of Port Edward is the southernmost record for the latter species, whereas *P. australis* occurs under estuarine conditions at the mouth of the Umtamvuna river (the north bank being the Natal border) and into the Transkei. Apart from this, the distributional patterns hardly differ. Population study suggests, however, that *P. australis* is the "older" established inhabitant, long-settled wherever suitable habitat conditions prevailed; only now being challenged and sometimes ousted, by what appears a more "aggressive", tropical competitor undoubtedly aided by the siltation of lower lying water courses that is the outcome, in part, of natural denudation, but mainly of man's mismanagement of land at higher altitudes.

The familiarity of the Zulu and Xosa people with the reed, "emhlanga", is reflected in the names of some of the rivers and villages in Natal and the Transkei.

SOUTH AFRICA. Over the remainder of the sub-continent the distributional pattern is yet more uncertain. Evidence is reasonably convincing that natural populations of *P. mauritianus* are not represented in the Cape Province, but it is a possibility that isolated ramets may have been planted there by human agency. This species, which is widespread in Rhodesia, Swaziland, the Transvaal (presumably Moçambique, though no records for this country have been verified in course of the present work) and Natal, is predominantly northern and eastern.

P. australis, on the other hand is southern and western, being well represented in the Cape Province and South West Africa. It is eastern also, as the frequency of Natal coast populations demonstrates. Its detailed distributional pattern further north is unclear, nor are its northern limits in the continent accurately established. It is difficult to believe, for instance, that the species is absent from Swaziland, while occurring in Rhodesia. Any collections of specimens that will help elucidate distributional limits will be greatly appreciated by the authors.

CONCLUSIONS

To some extent the present study has served to emphasize differences between the two taxa already recorded by previous authors (Hubbard, 1937: Clayton, 1967). In addition it has revealed further points of difference especially in populations in the field, so that on the basis of deeper knowledge of the plants from a wider range of aspects, identification has become easier.

The present study has also shown that while habitat conditions do modify some features of morphological form, the pungency of apices to leaves of axillary buds in particular, under the sub-tropical to warm-temperate environments prevailing in Natal and associated areas, populations and the plants of which they are composed, are clearly referable to one or other taxon. No evidence was obtained of plants or populations that were intermediate.

The further morphological and the anatomical differences disclosed, the habitat preferences revealed, and the more southern distribution of *P. australis*, all support the established concept that two taxa are represented. Absence of putative hybrids, sympatric association without loss of identity, and differences in ploidy are all suggestive of lack of gene exchange between them. This apparent genetic isolation, if eventually demonstrated experimentally, will provide irrefutable supporting evidence for the application of specific rank to which category both entities are already assigned.

KEYS TO SPECIES

1. *For use in the field*

Leaf blade and sheath deciduous: shed from the stem by an abscission zone developed at the base of the sheath: internode thus eventually naked with axillary bud exposed (most readily seen in the lower half of flowering stems). Axillary bud hardly recessed into stem tissue, oval without a basal pediment. Mature stems usually bearing one to several expanded axillary shoots with leaves with pungent apices. Leaf blades to mature stems yellowish green, hard, not rolling soon after detachment from sheaths, apices attenuate, firm. Panicles lax with markedly drooping branches, at maturity not invested by the uppermost stem leaf . . . . *P. mauritianus*

Leaf blade only deciduous: shed from the stem by an abscission zone developed at the junction of sheath and blade: internode and axillary bud thus persistenly invested by the leaf sheath (most readily seen in the lower half of flowering stems). Axillary bud (when exposed by artificial removal of sheath) recessed into stem tissue, round, with basal pediment. Mature stems usually lacking expanded axillary shoots (except when stem apex previously damaged). When axillary shoots are present, apices to the leaf blades are firm, but never pungent. Leaf blades to mature stems bluish, rolling soon after detachment from sheaths, apices long filiform, flexuous. Panicles compact, branches slightly drooping, at maturity usually invested by the uppermost stem leaf . . . . . . *P. australis*

2. *For use in the herbarium*

Upper glume 3·0—5·7 mm long. Sum of lengths of lower glume, upper glume and first (lowest) lemma 10·2—19·7 mm. Mature leaves hard, apex attenuate, firm. Abaxial epidermis of leaf blade with scattered outgrowths in the form of: (1) prickle hairs over the veins, (2) microhairs between the stomatal bands and the veins (fig. 16) . . *P. mauritianus*

Upper glume 5·0—9·2 mm long. Sum of lengths of lower glume, upper glume and first (lowest) lemma 18·3—27·0 mm. Mature leaves soft, apex long filiform, flexuous. Abaxial epidermis of leaf blade with scattered outgrowths in the form of: (1) unpointed prickles over the veins, (2) hooks between the veins, most frequent amongst the stomata, each hook usually paired with a cork cell (microhairs have never been observed) (fig. 17) *P. australis*

Summary of the More Important Differences between the Species

P. mauritianus	*P. australis*
Legehalme (non rigid runners of indefinite length) never observed	Legehalme produced by plants colonizing exposed mud banks, or growing in brackish water
Horizontal rhizomes terete	Horizontal rhizomes somewhat flattened dorso-ventrally
Mature photosynthetic leaf blades yellowish green, hard, not rolling immediately on detachment from sheaths, apices attenuate, but not long filiform and flexuous	Mature photosynthetic leaf blades bluish, soft, rolling immediately on detachment from sheaths, apices long filiform and flexuous
Distal leaves of actively growing sterile shoots with fine, white, erect hairs behind ligule (usually shorter and fewer than in *P. australis*, occasionally lacking)	Distal leaves of actively growing sterile shoots with long, coarse, white, erect hairs behind ligule
Sheath mouth with dense tufts of short white trichomes	Sheath mouth hairy, but without dense tufts of short, white trichomes
Lower leaves of aerial stems deciduous: each blade and sheath falling together leaving internode naked and axillary bud exposed	Blades only, of leaves of aerial stems, deciduous: each sheath persistent, investing internode and axillary bud
Abscission zone developed at base of leaf sheath	Abscission zone developed at base of leaf blade
Axillary buds hardly recessed into stem tissue, oval, without basal pediment	Axillary buds recessed into stem tissue, round, with basal pediment
Mature aerial stems with few to many expanded axillary shoots	Mature aerial stems usually without expanded axillary shoots
Apices of leaves to axillary shoots pungent	Apices of leaves to axillary shoots soft, never pungent (firm to hard, but not penetrating under brackish or xeric habitat conditions)
Inflorescences lax, with strongly drooping branches: usually more than 6 leaves persisting below each inflorescence, not lying in a single plane, uppermost not sheathing inflorescence base	Inflorescences compact, with slightly drooping branches: 6 or fewer leaves persisting below, often lying in a single plane, uppermost usually sheathing inflorescence base
Stems bearing old inflorescences dying back distally only: otherwise remaining photosynthetic	Stems bearing old inflorescences dying back to ground level
Spikelets of 3—7 (4, 5) florets	Spikelets of 3—9 (5, 6) florets
Upper glume 3·0—5·7 (mode 4·0) mm long	Upper glume 5·0—9·2 (mode 7·0) mm long
Sum of lengths of lower and upper glume and first lemma 10·2—19·7 mm	Sum of lengths of lower and upper glume and first lemma 18·3—27·0 mm
Abaxial epidermis of leaf blade with outgrowths from epidermal cells in form of: (1) prickle hairs, scattered over the veins in particular, (2) micro-hairs, thinly scattered between the stomatal bands and the veins	Abaxial epidermis of leaf blade with outgrowths from epidermal cells in form of: (1) unpointed prickles over the veins (no prickle hairs seen), (2) hooks (as distinct from prickle hairs) between the veins, most frequent amongst the stomata, each hook usually paired with a cork cell (microhairs never observed)

Citation of Material Studied

Both species have been adequately described by other authors, so it is not considered necessary to re-describe them here, especially as significant features by which they may be distinguished have been emphasized in the keys provided and in the summary of differences. Populations studied in detail are listed in tables 1 and 2, together with a brief résumé of habitat conditions in each case. Other populations studied in the field and from which herbarium specimens were obtained are listed below. Complete sets of all numbers prepared during the present work are deposited in the herbaria of the University of Natal, Pietermaritzburg, and University College, Durban (population samples: University of Natal only).

The additional herbarium specimens studied are not cited, as the material consisted, with few exceptions, of the distal tips of flowering stems. However, to give some guide to the distribution of each species in southern Africa as this is known at present (excluding Natal for which province distribution maps are provided: figs. 18a, b), countries or provinces, and where possible magisterial districts, from which specimens have been seen and could thus be identified with one or other taxon according to the criteria of difference presented here, are also listed.

Phragmites mauritianus Kunth, Rev. Gram. I: 277 (1830); Hubb. in Hill, Fl. Trop. Afr. X, I: 155 (1937); Chippindall, Grasses and Pastures of S. Afr.: 229 (1955); Clayton, Kew Bull. 21, 1: 117 (1967).

Other populations studied in the field

2930 (Pietermaritzburg) Pietermaritzburg (-CB), banks of Umsindusi River. *Gordon-Gray 6153;* Durban Bluff (-DD), on flats on road to Wentworth Hospital. *Gordon-Gray 6156A;* Isipingo North (-DD), 29°59′S, 30°57′E *Ward 6580;* Isipingo North (-DD), 29°59′S, 30°57′E *Ward 6591;* Isipingo Flats (east) (-DD), 29°59′S, 30°57′E former course of Mlazi River *Ward 6552;* 3030 (Port Shepstone) Mpenjathi River (-CD) 30°58′S, 31°16′E main S. Coast road bridge *Ward, 6757.*

Localities verified

Angola: South West Africa (Amboland): Transvaal (Pietersburg, Waterval Boven and Nelspruit distrs.): Swaziland (Pigg's Peak, Mbabane and Hlatikulu distrs.).

Phragmites australis (Cav.) Trin. ex Steud., Nom. Bot. ed. 3, 2:324 (1841); Clayton, Taxon 17, 2:168 (1968).

P. communis Trin., Fund. Agrost.: 134 (1820); Stapf, in Thiselt.-Dyer Fl. Cap. 7:541 (1898); Hubb. in Hill, Fl. Trop. Afr. X, 1:153 (1937); Chippindall, Grasses & Pastures of S. Afr.: 228 (1955); Clayton, Kew Bull. 21, 1:116 (1967).

Other populations studied in the field

2929 (Underberg) Tabamhlope Research Station (-BA) in stream *Gordon-Gray 6281;* Mooi River (-BB) north bank of river in the town *Gordon-Gray 6280;* 2930 (Pietermaritzburg) Umgeni River, Midmar Dam (-CA) downstream of main dam wall *Gordon-Gray 6160A;* Wentworth (-DD) swamp near S.A.R. station 29°54′S, 30°49′ E *Ward, 6578;* Isipingo Beach (-DD) 29°59′S, 30°56′E *Ward, 6583;* ditto *Ward 6594; 6595; 6764; 6763;*

2930 (Pietermaritzburg) Isipingo River (-DD) 29°59′S, 30°56′E *Ward, 6598;* Isipingo Flats (east: former course of Mlazi River 29°59′S, 30°57′E *Ward, 6550; Ward 6551;* 2930 (Pietermaritzburg) Isipingo North 29°58′S, 30°57′E *Ward, 6592;* Isipingo North 29°59′S, 30°57′E *Ward, 6585.*

LOCALITIES VERIFIED

South West Africa (near Namutoni; near Grootfontein; near Swakopmund; near Windhoek): Orange Free State (Bloemfontein distr.): Lesotho (Leribe distr.): Cape Province (Umzimkulu, Mount Currie, Umtata, Idutywa, Kentani, Komgha, Kingwilliamstown, Albany, Port Elizabeth, Humansdorp, Middelburg, Uitenhage, Joubertina, Knysna, George, Uniondale, Oudtshoorn, Riversdale, Swellendam, Stellenbosch, Worcester, Simonstown, Malmesbury, Clanwilliam, Herbert and Barclay West distrs.).

Subsequent field work by one author, CJW, has revealed the presence of *P. mauritianus* at several localities in the Transkei, the southernmost being the Bashee Bridge where the main Transkei-Cape road crosses the Bashee river.

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